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Presence of two cave bear species in La Lucia cave (Lamasón, Cantabria, N Spain): *Ursus deningeri* von Reichenau and *Ursus spelaeus* Rosenmüller-Heinroth

Presencia de dos especies de oso de las cavernas en la Cueva de la Lucia (Lamasón, Cantabria, N de España): Ursus deningeri von Reichenau y Ursus spelaeus Rosenmüller-Heinroth

KEY WORDS: Pleistoceno, *U.deningeri, U. spelaeus,* morphology, metrical analysis, AAR dating, 9th OIS, 5th OIS.
PALABRAS CLAVE: Pleistoceno, *U.deningeri, U.spelaeus*, morfología, análisis métrico, datación AAR, 9º OIS, 5º OIS.

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RESUMEN

Se presenta el estudio paleontológico sistemático y tafonómico de dos acumulaciones de dientes y huesos de osos fósiles de la Cueva de la Lucia (Lamasón, Cantabria). Los restos de oso se localizaron en dos sitios distintos de la cueva: La Sala (LUS) y La Rampa (LUR). El inventario general de hallazgos y el cálculo de edades a partir del desgaste dentario revelan que en LUR, una parte remota de la cueva sin acceso directo, se han encontrado abundantes restos de *U.deningeri* que testimonian un largo periodo de colonización por individuos jóvenes y adultos. En LUS, una zona directamente conectada con el exterior, dominan los restos de individuos subadultos, oseznos y recién nacidos. La datación numérica de los yacimientos mediante U/Th. Resonancia de Espíen Electromagnético (ESR) y racemización de aminoácidos, sitúa la acumulación de restos de *U.deningeri* en el 9º Episodio del Oxígeno Marino, mientras que los restos de *U.spelaeus* se acumularon durante el 5º Episodio del Oxígeno Marino (5º OIS). Los estudios morfológicos y métricos del material permiten una clara clasificación paleontológica de los materiales, confirmando el carácter ancestral de *U.deningeri*. Los metapodios de *U.spelaeus* muestran un marcado dimorfismo sexual, menos marcado en *U. deningeri*. En nuestra opinión el importante recorrido de las diversas medidas tomadas en los molariformes, hacen inviable establecer nuevas subespecies, más todavía especies, en base a un material poco abundante.

ABSTRACT

We present the taphonomical and palaeontological study of two fossil bear bone and teeth accumulations from La Lucia Cave (Lamasón, Cantabria). The bear remains were located in two different sites: the Ramp (LUR) and the Hall (LUS). The general inventory of findings and the age calculation from dental wear revealed the following: in LUR, a remote part of the cave with no direct entrance, abundant *U. deningeri* remains were found, attesting a long colonization period; both adult and young representative remains were recovered. In the LUS site, which is clearly connected to the open air, only sub-adult, cub and newborn remains were found. Numerical dating through U/Th, electron spin resonance and amino acid racemization placed the *U. deningeri* accumulation at the 9th OIS, while *U. spelaeus* remains were accumulated during the 5th OIS. Morphological and metrical analysis enabled clear palaeontological identification, and confirmed that the *U. deningeri* species was the direct ancestor of *U. spelaeus*. *U. spelaeus* metapodials showed a highly marked sex dimorphism which was less evident in *U. deningeri*. In our opinion the important range observed in the measurements taken of cheek teeth makes it very difficult to establish new subspecies, or even more species, based on a reduced number of findings.

LABURPENA

Cueva de la Lucia leizeko (Lamasón, Kantabria) hartz fosilen hortz eta hezur metaketa pare baten azterketa paleontologiko sistematiko eta tafonomikoa aurkezten da. Hartz aztarnak leizeko bi tokitan aurkitu ziren: La Sala (LUS) eta La Rampa (LUR). Aurkikuntzen inbentario orokorrak eta hortzen higaduratik abiatutako adin kalkuluak leizeko barne-barneko eta zuzeneko sarbiderik gabeko tokia den LURren *U.deningeri*-ren hondakin ugari aurkitu dela, indibiduo gazte eta helduek kolonizazio luzea egin zutelako adierazgarri. LUSen, kanpoaldearekin zuzenean konektaturiko eremua den horretan, ez helduen, hartz-kumeen eta jaioberrien aztarnak nagusi dira. Aztarnategien zenbaki datazioa U/Th-ren bitartez. Espíen Elektromagnetikoaren Erresonantzia (ESR) eta aminoazidoen errazemizazioa, *U.deningeri*-ren aztarnen metaketa Itsas Oxigenoaren 9. Episodioan kokatzen du, *U.spelaeus*-en aztarnak, berriz, Itsas Oxigenoaren 5. Episodioan (5. OIS) metatu ziren. Materialaren azterketa morfologikoek eta etrikoek materialen sailkapen paleontologiko argia ahalbidetzen dute eta, horrela, *U.deningeri*-ren antzinakotasuna berresten dute. *U.spelaeus*-en metapodioek sexu diformismo nabaria erakusten dute, *U.deningeri*-n ez hain markatua. Gure aburuz, molariformeetan harturiko neurrien ibilbide garrantzitsuak subespezie berriak ezartzea ezin bideratuzkoa egiten du, are gehiago espezieak, material ez oso ugaria oinarri.

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INTRODUCTION

In 1989, during an exploratory campaign in the Sierra de la Collada massif, a new cave, La Lucia cave, was discovered by the Bathynellidae Speleological Group. The cave hosted exciting palaeontological findings consisting of large accumulations of cave bear remains cropping out in two different cave sites. The speleologists recovered some samples and their study revealed to be of sufficient interest to justify an excavation. Three excavation campaigns were carried out from 1993 to 1995. This paper presents our results on: the age of the two cave bear remains accumulations; the inventory of findings as a key for cave bear site taphonomy; an approach to age at death and minimum number of individuals; and morphological and metrical study of fossil bear remains.

Geographical and geological settings

La Lucia cave (X=376,850 E; Y= 4.793,240 N; Z= 500 m. asl) lies inside the Arria area of the Sierra de la Collada massif, near the Lamasón valley and the small village of Sobrelapeña (province of Cantabria, Northern Spain) (figure 1).

The main morphological feature of the study area is the Latarmá River, which flows in W-E direction along a narrow valley deeply incised in the eastern part of the massif. This valley was probably the result of the tardive evolution of an underground drainage network which, after a climate-linked water level fall, changed from batyphreatic to epigean-epiphreatic conditions. In the river talweg a string of small caves where the river stream sinks supports this interpretation.

Along the river valley there are many subterranean and epigean tributaries. One of the most prominent is a karstic valley called Canal del Arcedillo; this is a dry valley which has its catchments, both epigean and subterranean, in the Acebal zone where large numbers of dolines and grikes (solution widened joints) are to be found. La Lucia cave opens near the confluence of the Canal de Arcedillo and the River Latarmá.

Like many other caves in the massif, and in spite of its reduced length (653 m), La Lucia cave shows very large circular-in-section galleries and fine speleothems.

At present, the main cave entrance consists of a 19 m deep open shaft, caused by a significant collapse of the cave gallery ceiling. A debris cone

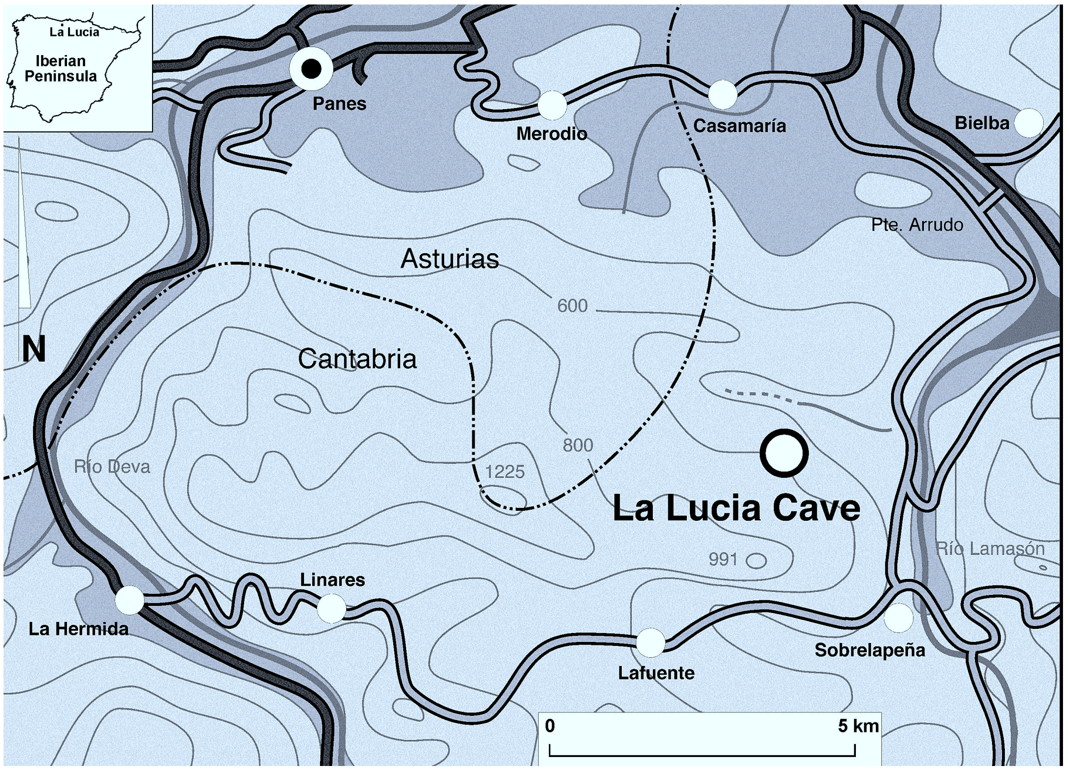

Figure 1. Geographical situation of La Lucia cave.

made of boulders and litter attests to this. Inside the cave this collapse produced an impressive hall (Megatherium hall). East of the Megatherium hall a wide but almost totally sediment-filled gallery was the ancient cave bear entrance to the hibernation site in the La Lucia Hall site (LUS); this is now a micromammal den, as hundreds of predated land snail shells attest (figure 2).

Towards the west the cave becomes quite impressive with abundant and attractive speleothems (stalactites, stalagmites and columns). Here, an 11 m high stepping wall made from flowstone connects with the Bears' Corridor. At this point the flowstone shows hundreds of bear claw-marks. Hollows dug for hibernation still remain in the Bears' Corridor and a young bear's articulated limb is sinter-cemented to the gallery floor. This corridor connects, through a narrow passage, with the Crystal Palace, a wide dome-like hall whose southern wall shows mud flow deposits rich in cave bear remains. The mud flow sediments finally accumulated forming a debris cone at the bottom of the Crystal Palace hall. There, an impressive amount of cave bear remains accumulated, although they have since been eroded by influent seepage waters (figure 2). We named this zone the La Lucia Ramp (LUR)

The sediments of the Ramp site (LUR) consist of crudely bedded loams with scattered angular-shaped limestone-in-nature boulders and gravel, and bear remains which reveal a deposition according to its critical slope. The sediments are water-saturated as a result of continuous laminar runoff due to the dripping from the site ceil ing, thus making it very difficult to excavate the dough-like mass. In the debris cone head the sediments are not water-saturated and appear more compacted.

The excavation at the hall site (LUS) was easier — the sediment was dry and soft — but the density of the findings was very low (see inventory). From bottom to top the section consisted of:

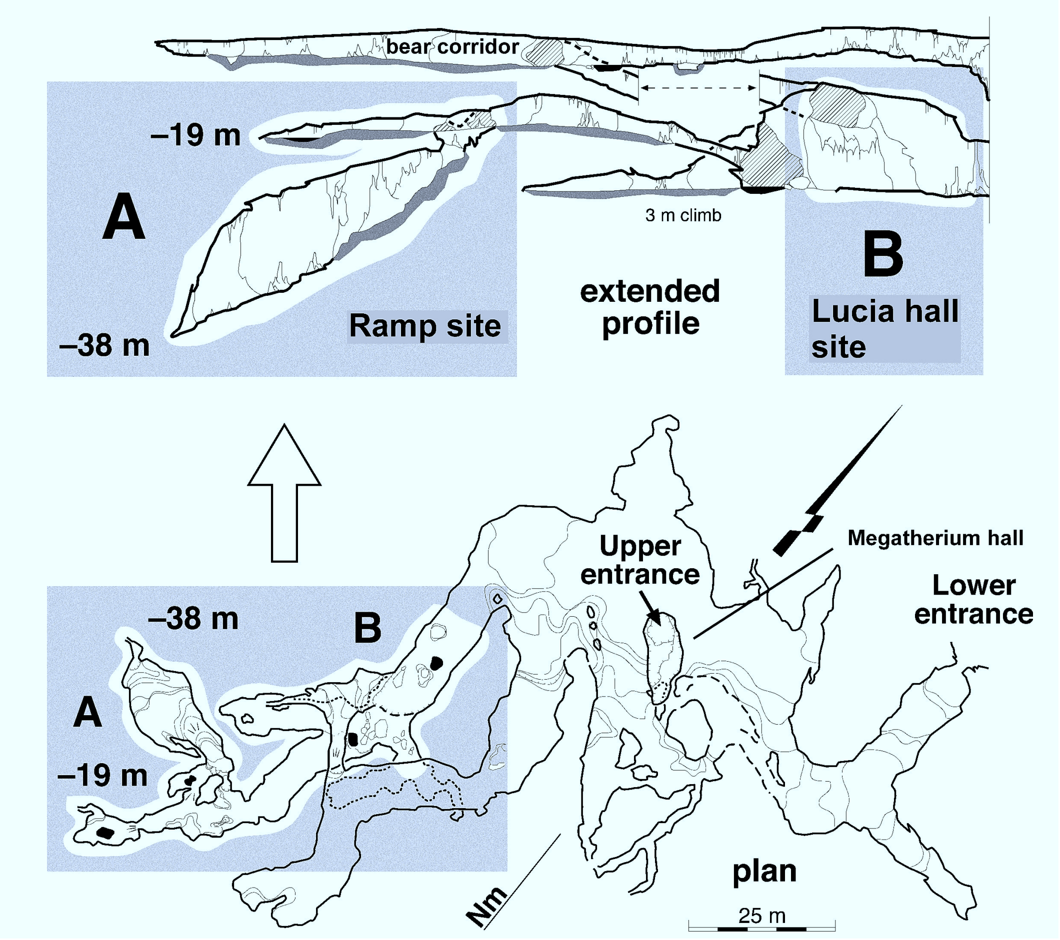

Figure 2. Plan view and section of La Lucia cave. Hall site (LUS) and Ramp site (LUR) are indicated.

- >80 cm of sterile (paleontological sense) reddish-brown cave loams and scattered calcareous gravel.
- 20 cm of cave loams with plenty of organic-coated water-filled bubbles. Scattered calcareous gravel.
- 20 cm of cave loams with *U. spelaeus* remains, with scattered fallen stalactites and calcareous gravel.
- 5 cm of flowstone.

The upper flowstone forms the speleological floor of the entrance gallery and the La Lucia Hall (LUS) site; it laterally changes into calcareous sinter and a shallow pond (gour). Deeply weathered cave bear bones appear here. Well preserved, recent spectacular stalagmites and columns also decorate this part of the cave.

Materials and Methods

For the dating of the two cave bear accumulations radiometric methods (Uranium/Thorium and Electron Spin Resonance) and geochemical methods (Amino Acid Racemization) were employed. U/Th dating was carried out on speleothems from the La Lucia Hall (LUS) site in the Institut Jaume Almera, part of Spain's Scientific Research Council. The Electron Spin Resonance dating was done on enamel samples from cave bear canines from the La Lucia Hall (LUS) site in the Australian National University. For amino acid racemization dating, a large number of dentine samples from canines and molars from both cave bear accumulations were taken. These analyses were carried out at the Biomolecular Stratigraphy Laboratory of the Madrid School of Mines.

The age at death was based on wear of premolars and molars according to the methods proposed by TORRES (1976) and STINER (1998).

Due to the scarcity of cranial and post-cranial findings, the morphological analysis was performed on premolars and molars. La Lucia bears frequencies of different morphotypes of cusps and teeth were compared with previously published data of Iberian *Ursus deningeri* (La Sima de los Huesos, Atapuerca-Burgos) and *Ursus spelaeus* (Ekain, Deba-Gipuzkoa and Reguerillo, Patones-Madrid) localities.

The metrical analysis was performed on metapodials, premolars and molars. Different representative measurements were compared with all the previously published data from all the Iberian localities. Bivariate analysis was widely used to characterize the bear species from La Lucia cave as well as to discuss the specific significance of *U. deningeri.*

RESULTS AND DISCUSSION

Dating

Fortunately, it was possible to date both cave bear accumulations through radiometric (Uranium/Thorium and Electron Spin Resonance) and geochemical (Amino Acid Racemization) methods. The obtained ages through these methodologies, (see Table 1) gave a more feasible guarantee of the previous palaeontological determinations.

The U/Th dating from the scattered stalactites found in the La Lucia Hall bear remains/bearing bed, and from the flowstone that seals the fertile strata gave the ages 76424±2700 BP and 77231±305 BP. This means that the growth and further fall of the small stalactites and the flowstone deposition were almost coeval. These radiometric data suggest that the bears colonized La Lucia cave at least prior to the 4th Oxygen Isotopic Stage (OIS) established by SHACKELTON (1967) in the marine record.

Santa Isabel (SI)	*U. deningeri*	Unpublished	ESR	305. ± 23BP
La Sima de los Huesos (BB)	*U. deningeri*	Bischoff *et al.* 1997		
La Lucia Hall (LUS)	This paper	U/Th Torres *et al.* (2002 a)	U/Th	76424±2700 BP 77231±305 BP
Eirós (EE)	*U. spelaeus*	Grandal d'Anglade Vidal Romaní (1997)	^{14}C	24090 ±440
Pasada (SS)	*U. spelaeus*	Unpublished	ESR	30.1± 1.8 BP 37.8±3.7 BP
Troskaeta (TR)	*U. spelaeus*	Unpublished	ESR	54.7±4.6 BP 68.4±4.9 BP
Amutxate	*U. spelaeus*	Unpublished	ESR	39±2 BP 48±3 BP

Table 1. Radiometric datings from La Lucia Hall (LUS) and some other Iberian localities.

The Electron Spin Resonance (ESR) dating on dental enamel of bear samples from La Lucia Hall site (LUS) indicates that the cave bear population colonized the cave during the 5th OIS, the obtained ages on five samples range between 111± 12 ka BP and 129±15 ka BP.

The use of amino acid racemization – aspartic acid from dentine collagen – requires previous radiometric calibration. In the present study we used different radiometric datings (see table below).

The age calculation from our calibrated mathematical algorithms (see table 2, and figure 3) confirms the radiometrical age of the La Lucia Hall bears, which results to be older than many typical *Ursus spelaeus* localities, but younger than other two (El Reguerillo and Arrikrutz caves). The La Lucia Ramp bears have been dated at 247 ± 26 ka BP, broadly coincident with the ages obtained from two Iberian *U. deningeri* sites (Santa Isabel cave and Sima de los Huesos); see TORRES *et al.* (2001) and TORRES *et al.* (2002 a, b, c).

These results imply that La Lucia cave was colonized twice. According to the OIS established by SHACKELTON (1967), the first colonization took place during the 9th OIS, and then after a time-gap of almost 200 ka the cave was re-colonized during the 5th OIS. This time gap explains why it seems impossible to reconstruct the former cave entrance to the La Lucia Ramp, now totally masked by a chaos of fallen rocks from the ceiling, speleothems and erosion under vadose-epiphreatic conditions.

Locality	Species	Age (OIS)
Santa Isabel (SI)	*U. deningeri*	9-10
La Sima de los Huesos (BB)	*U. deningeri*	9
La Lucia Ramp (LUR)	This paper	9
Reguerillo (TT)	*U. spelaeus*	6
Arrikrutz (AA)	*U. spelaeus*	6
La Lucia Hall (LUS)	This paper	5
El Toll (XX)	*U. spelaeus*	3
La Pasada (SS)	*U. spelaeus*	3
Troskaeta (TR)	*U. spelaeus*	3
Amutxate (AX)	*U. spelaeus*	3
Los Osos (TE)	*U. spelaeus*	3
Eirós	*U. spelaeus*	3-2
Ekain (KK)	*U. spelaeus*	3-2

Table 2. Amino acid racemization-based chronostratigraphy from La Lucia cave bear remains and other Iberian localities.

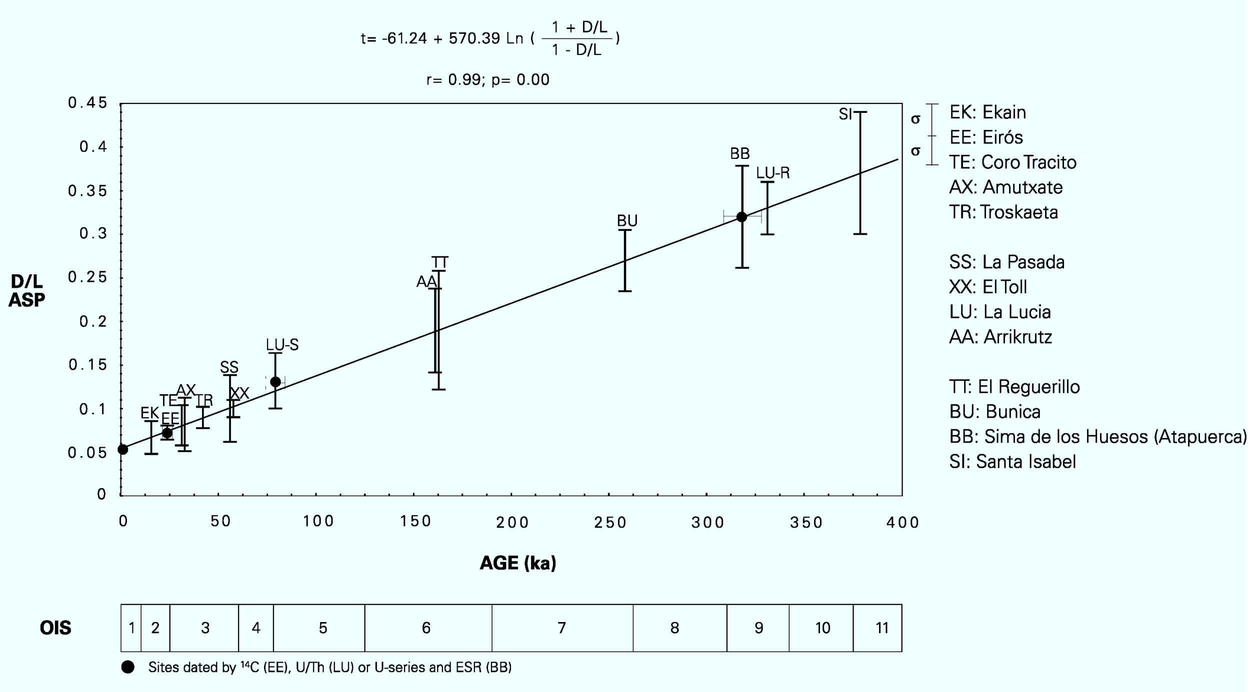

Figure 3. Calibrated age calculation from Aspartic Acid Racemization ratios.

Inventory of findings

After the excavation campaigns several hundreds of well-preserved bear remains were recovered. Table 1 presents the general inventory of findings. The main components of skeleton and dentition have only been identified with an indication of their age at death (a= adult; j= juvenile + yearling + newborn remains) (see tables 3, 4 & 5). As is usual in cave bear sites no other general representatives were found. From these tables some initial conclusions can be drawn:

In the Hall site (LUS) a clear predominance of non-adult bear remains was found, while in the Ramp site (LUR) adult bear remains are best represented.

In the Ramp site inventory (LUR) a marked increase in the frequency of "fragments" appears, suggesting that there are large amounts of unidentifiable bony fragments representing a negligible part of the complete anatomic component; this can be explained by these having being transported a greater distance.

According to the detailed inventory of well preserved (measurable element) remains, (tables 2 and 3), the minimum number of individuals is 22 for the bear remains accumulation at the La Lucia Ramp (LUR) site (M^1 sin.). At the La Lucia Hall (LUS) site a minimum number of 12 individuals (M2 dex.) was recorded. The reduced number of recovered adult skeletal remains in the La Lucia Hall (LUS) site is noteworthy.

Age at death

A rough approximation to the age at death can be made from the wear degree of premolars and molars (TORRES, 1976; STINER, 1998). Although the counting of cement accretion bands seems to be a more precise system, we decided to use only teeth wear stages (degrees) to determine the age at death of La Lucia bears, following the four categories established in TORRES (1976)

Stage I: teeth that do not show any trace of wear. All the cusps are intact but in some cases very small wear facets are visible under oblique light. Usually the roots are largely open and undeveloped.

Stage II: teeth with minor traces of wear; wear facets are clearly visible and small spots of dentine can outcrop inside. The roots are totally developed but the apices may remain open.

	LUR		LUS	
Total findings	2417		642	
Skull (fragments)	141	(91 j. 50 a.)	59	(39 j. 20 a)
Mandible (mostly fragments)	55	(20 j. 35 a.)	44	(32j. 12 a.)
Vertebrae	190	(26 j. 164 a.)	22	(7 j. 15 a.)
Ribs	220	(84 j. 136 a.)	118	(90 j. 28 a.)
Scapula (fragments)	34	(9 j. 25 a.)	10	(5 j. 5 a.)
Humerus (complete & fragments)	72	(32 j. 42 a.)	35	(30 j. 5 a.)
Ulna	59	(16 j. 43 a.)	27	(22 j. 5 a.)
Radius	58	(23 j. 35 a.)	18	(18 j. 0 a.)
Carpal bones	36 a.			
Metacarpal bones (adult only)	34		5	
Phalanx	136	(25 j. 111 a.)	18	(0 j. 18 a.)
Pelvis	34	(21 j. 13 a.)	29	(15j. 14 a.)
Femur	98	(56 j. 42 a.)	39	(35 j. 4 a.)
Tibia	45	(26 j. 19 a.)	29	(23 a. 6 j.)
Fibula	9	(2 j. 7 a.)	9	(7 j. 2 a.)
Tarsal bones	57	(0 j. 57 a.)	5	(0 j. 1 a.)
Metatarsal bones	47	(0 j. 47 a.)	5	(0 j. 5 a.)
Sesamoids	19	(0 j. 19 a.)		
Metapodials (juvenile)	51		6	
Articular (juvenile)	11		2	
Dentition	305		87	
Dentition (decidual)	16		4	
Other	5			
Fragments	685		71	

Table 3. General inventory of skeletal remains from La Lucia cave bear accumulations according to their age at death.

	LUR			LUS		
	Sin.	Dex.	Ind.	Sin.	Dex.	Ind.
Mandible	3	7			2	
Atlas			6			1
Axis			2			
Scapula	5	5	1		1	
Humerus	15	7		1	5	
Ulna	16	5	1	1	1	
Radius	8	13				
Scapholunate	4	3		1	1	
Hamate	4	1				
Capitate	2	5				
Pisiform	4	6				
Triquetral		1				
Trapezium	2	1				
Trapezoid		1				
1st Metac.	1	5				
2nd Metac.	3	1				
3rd Metac.	4	3		1		
4th Metac.	6	4		1	1	
5th Metac.	4	3		2		
1st Phalanx.			56			
2nd Phalanx.			29			
3rd Phalanx.			18			
Pelvis	2	4		2	1	
Femur						
Patella	5	2			1	
Tibia	7	8	1	2	1	
Fibula	5	8	2			
Calcaneum	6	6		1		
Astragalum	9	9			1	
Cuboid	3	3		1		
Scaphoid	9	6			1	
Med. Cun.						
Centr. Cun.		1				
Lat. Cun.	2	3			1	
1st Metat.	3	7			1	
2nd Metat.	4	2			1	
3rd Metat.	2	5				
4th Metat.	2	7		1	1	
5th Metat.	8	7			1	

Table 4. Inventory of skeletal remains of adult bears from La Lucia cave bear accumulations

	LUR			LUS		
	Sin.	Dex.	Ind.	Sin.	Dex.	Ind.
Upper canine	4	5	3			
1st Upper inc.	10	0				
2nd Upper inc.	6	8				
3rd Upper inc.	11	12	3			
4th Upper premolar	3	8		2	4	
1st Upper molar	22	18		5	5	
2nd Upper molar	11	8		3	6	
Lower canine	9	8	3	1	3	
1st Lower inc.	3	4				
2nd Lower inc.	3	3				
3rd Lower inc.	8	5				
4th Lower premolar	5	11		4	10	
1st Lower molar	18	18		2	4	
2nd Lower molar	17	19		11	12	
3rd Lower molar	11	11		8	9	
Canine ind.			17			

Table 5. Inventory of dental remains from La Lucia cave bear accumulations.

Stage III: teeth with severe damage, dentine crops out in less than 50% of the occlusal surface of the crown. The roots are closed.

Stage IV: wear affects more than 50% of the occlusal area of the crown. Deep wear notches appear and there is evidence of in vivo tooth breakdown. Root channel ends are visible on the dismantled crown. The roots are closed.

The results of the wear analysis are shown in table 6. It is noteworthy that all the premolars and molars from La Lucia Hall (LUS) belong to Group I: they do not show any trace of wear. This means that the cave bear individuals were young, cubs or immature; this is consistent with the distribution of skeleton elements (see table 4), where a very marked dominance of elements from "juvenile" representatives (newborns + cubs + juvenile) can be observed. The wear stage distribution in the sample from La Lucia Ramp (LUR) also reveals a clear dominance of Group I, although there is a group of adult bear representatives. In any case, this type of age at death distribution is typical of that found in cave bear sites. Only one *Ursus spelaeus* locality (Arrikrutz cave, Oñati, Gipuzkoa) reported by TORRES (1976) showed a different age at death distribution, the difference being due to the predominance of old individuals.

Wear degrees	LUS	LUR			
	I	I	II	III	IV
P^4	6	14	1		2
M^1	10	32	3	2	3
M^2	8	11	4	2	1
P_4	9	17	1		1
M_1	7	26	4	3	2
M_2	18	33	1	1	5
M_3	18	20	4	3	

Table 6. Age at death calculation from wear stages of premolars and molars from La Lucia Hall and La Lucia Ramp bears.

Morphological analysis of premolars and molars

Because the dentition of speloid bears (*U. deningeri* and *U. spelaeus*) shows a marked — and at times astonishing — morphological plasticity it is very difficult to establish morphological characteristics for species distinction. Premolar and molar morphology of the La Lucia cave bears were compared with the morphologies found in *Ursus deningeri* from La Sima de los Huesos (BB-Atapuerca, Burgos), and *Ursus spelaeus* from El Reguerillo (TT-Reguerillo cave, Madrid) and Ekain cave (KK-Deba, Gipuzkoa). These morphotypes were established following MUSIL (1959) and modified in TORRES (1989)

As it can be seen in table 7 there are no marked differences between the P^4cusp morphologies of La Lucia Ramp (LUR) bears and those of *U. deningeri* from La Sima de los Huesos (BB). The frequencies of metacone and deuterocone morphotypes from the La Lucia Hall (LUS) are consistent with those from El Reguerillo (TT).

As the morphology of the cusps of the first upper molar (see table 8) is very conservative, no special differences were found, although the M^1 of bears from La Lucia (LUR) shows a high frequency of cases where the parastyle is lacking, as also occurs for *U. spelaeus* from Ekain (KK) and Reguerillo (TT). The morphologies found at the cusps from the first upper molar of La Lucia Hall (LUS) bears do not differ from those from other Iberian localities with *U. spelaeus*.

The morphology of the outline of the crown (see table 9) from the M^2 of La Lucia Hall (LUS) bears does not differ from frequencies found in other Iberian sites with *U. spelaeus (*TT and KK). The M^2 crowns from La Lucia Ramp (LUS) show acute tips (talus), as observed in *U. deningeri* from La Sima de los Huesos (BB); this reflects the lack of relative overdevelopment of the M_3, as is typical in *U. spelaeus.* The second upper molars from La Lucia Hall (LUS) show a total dominance of typica*l U. spelaeus* molar outline morphologies.

P^4 Cusp morphology		LUR	*U. d.* BB	LUS	*U. s.* KK	*U. s.* TT
Paracone	Single	8	86	5	94	46
	W. parastyle	3		1	3	2
Metacone	Single	9	73	1	17	4
	W. metastyle	2	13	5	80	43
Deuterocone	Single	9	77	6	47	40
	Duplicated	2	9		50	7

Table 7. Morphotypes of the cusps of the fourth upper premolar. BB-Sima de los Huesos (Atapuerca), KK-Ekain Cave (Deba), TT- Reguerillo Cave (Madrid).

M^1 Cusp morphology		LUR	*U. d.* BB	LUS	*U. s.* KK	*U. s.* TT
Paracone	Parastyle	27	70	9	71	10
	Small parastyle	10	3	1	28	44
Protocone	W. metaconule	35	70	8	67	53
	Small metaconule	2	24		1	
	Complex		5	2	28	1
Metacone	W. metastyle	29	93	3	73	51
	Metastyle absent	1	1	1	4	
Hipocone	Small metastyle	7		6		1
	Single	36	99	10	98	45
	Complex	1	1		1	10

Table 8. Morphotypes of the cusps of the first upper premolar. BB-Sima de los Huesos (Atapuerca), KK-Ekain Cave (Deba), TT- Reguerillo Cave (Madrid).

The morphologies from the M^2 cusps (see table 10) from La Lucia Hall (LUS) are fully consistent with those found in *U. spelaeus* from Ekain (KK) and El Reguerillo (TT). In the second upper molars from the La Lucia Ramp (LUR) there is an important number of cases where the metaconule is absent (undifferentiated), as it can be observed in La Sima de los Huesos (BB) representatives. The morphologies of the cusps of the second upper molar from La Lucia Hall (LUS) representatives matched especially well with those from Ekain (KK).

In the P_4 of bears from the La Lucia Ramp (LUR) the paraconid is frequently absent or appears as a single, low blunt enamel dome (see table 11). This also occurs in *Ursus deningeri* from La Sima de los Huesos, and in *Spelaearctos deningeri kudarensis* BARYSHNIKOV from Kudaro cave in Transcaucasia (Georgia) (see BARYSHNIKOV 1998). These morphologies, although present, are uncommon in *U. spelaeus*. There is also a conspicuous presence of a small cusplet on the posterior tip of the crown, this cusplet being bigger in *U. spelaeus*; in Ekain (KK) representatives this cusp appears as high as the main cusp of the paraconid amassment of cusps.

Two fourth lower premolars from the La Lucia Ramp (LUR) show fused roots. This characteristic appears indistinctly in both cave bear representatives from La Lucia cave (Hall and Ramp sites). According to TORRES *et al*. (1991) this character was common in the *U. s. parvilatipedis* TORRES from Troskaeta cave (Ataun, Gipuzkoa). The morphologies from the fourth lower premolar from La Lucia Hall (LUS) seem to be quite similar to the morphologies found in other cave bear populations, although there is a marked presence of premolars with complex paraconids.

M^2 Crown outline	LUR	*U. d.* BB	LUS	*U. s.* KK	*U. s.* TT
Oblique labial side of the crown and acute talus tip	5	25	2	9	9
Labial side of the crown Straight lingual side convex and acute talus tip. Notch between paracone and metacone.	4	13			
Rounded talus tip and notch between paracone and metacone	4	59	5	70	42
Rounded talus tip. Straight labial side of the crown	1	37		29	14

Table 9. Morphotypes of the outline of the crown of the second upper molar. BB-Sima de los Huesos (Atapuerca), KK-Ekain Cave (Deba), TT- Reguerillo Cave (Madrid).

M^2 Cusp morphology		*U. d.* LUR	BB	*U. s.* LUS	*U. s.* KK	TT
Paracone	Single	14	53	7	92	47
	W. parastyle	1	11	1	8	
Protocone	W. metaconule	13	52	8	100	45
	Metaconule absent	2	12			2
Metacone	Single	7	4	4	56	1
	Duplicated	8	51	3	44	46
	Complex		9	1		
Hipocone	Single	2	1	1	17	2
	Duplicated	10	44	6	45	41
	Complex	3	19	1	8	4

Table 10. Morphotypes of the cusps of the second upper molar. BB-Sima de los Huesos (Atapuerca), KK-Ekain Cave (Deba), TT- Reguerillo Cave (Madrid).

In the first lower molars (see table 12) from the La Lucia Ramp (LUR) half of the paraconids present the "ursavoid" morphology. This cusp shape leads back to the remote bear ancestors (Genus Ursavus), where the paraconid looked like a sharp vertical enamel blade (TORRES, 1988). In recent (Pleistocene) Ursidae this enamel blade became increasingly blunt while tilting toward the lingual side of the tooth. Finally, in *U. spelaeus,* it changed into a tilted backward surface which was plate ridge-limited and triangular-shaped, giving it a clear complementary crushing functionality. This morphology is uncommon in both *U. spelaeus* and *U. deningeri,* but it was quite often found in *U. s. parvilatipedis* representatives from Troskaeta cave (TORRES *et al.*, 1991). A more evolved "Ursavoid" (the morphology of this cusp) paraconid is observable in the lower carnassial (d3) of the decidual dentition, which looks like a sharp-pointed cone rather than a sharp blade. The more conservative character of the deciduous dentition has been suggested in the genus *Arctotherium* by SOIBELZON & CARLIN (2004).

Both the second lower molar and the first upper one are very conservative and not very important differences were found (see table 13). The paraconid area, where there is no definite cusp, shows a string of enamel beads enclosing a flat zone covered with bubblets and ridges of enamel. The number of beads (blunt cusplets) is variable; the simplest morphologies dominate in *U. deningeri,* and also in *U. spelaeus* with the exception of Ekain (KK) representatives, which have more complex morphologies.

P_4 Cusp morphology	LUR	*U. d.* BB		*U. s.* LUS	*U. s.* KK	TT
Paraconid	Absent	5	2			
	Simple	3	7		3	2
	Duplicated (1)	10	19	5	96	34
	Complex (1)	1	8	4	12	6
Protoconid	Simple	19	36	9	113	42
Talonid	Cusp. At the Posterior tip of the Crown (2)	10	34	7	68	19
	Latero-internal cusplet (3)	11	70	9	81	21
Root	Fused	2	11	2	2	

Table 11. Morphotypes of the cusps of the fourth lower premolar. BB-Sima de los Huesos (Atapuerca), KK-Ekain Cave (Deba), TT- Reguerillo Cave (Madrid).

M_1 Cusp morphology		LUR	*U. d.* BB	LUS	*U. s.* KK	*U. s.* TT
Paraconid	"Ursavoid"	14				
	Simple	28	27	1	121	36
	Complex		1	6	13	9
Protoconid	Simple	12	18	7	18	21
	Posterior cusplet	5			111	21
	Two post. cusplets	6	10		5	2
Metaconid	Two cusps	8	2		52	18
	Three cusps	12	14	5	57	18
	Double w. cusplets	1	11	1	5	3
	Single w. cusplets	7	2	1	10	5
Entoconid	Double	4	4	3	73	13
	Double w. cusplets	23	24	4	61	31
Hypoconid	Simple	11	3			
	W. hypoconulid	16	24	7	134	107

Table 12. Morphotypes of the cusps of the first lower molar. BB-Sima de los Huesos (Atapuerca), KK-Ekain Cave (Deba), TT- Reguerillo Cave (Madrid).

No important differences were found in the protoconid and metaconid morphologies, although *U. spelaeus* from Ekain (KK) shows more complex forms. The metaconid morphologies are highly variable in *U. deningeri* from La Sima de los Huesos (BB) and in the La Lucia Ramp (LUR) bear. There is a tendency toward baroque forms with many accessory cusplets due to the atomization of the main cusps. In *U. spelaeus* there is a predominance of forms composed of 2-3 bigger sized cusps due to an occlusal area augmentation.

In *U. deningeri*, entoconids made of three cusp-complex *"en ecaliere"* predominate, as KOBY (1951) noted. In *U. deningeri*, hypoconulid is absent in many cases, as observed in both La Lucia Hall (LUS) and La Lucia Ramp (LUR) molars.

In M_3 only the general (occlusal) crown outline could be analyzed because cusps appear as masses of cusplets and ridges (see table 14). Among the La Lucia Ramp (LUR) and La Sima de los Huesos (BB) representatives, there is a conspicuous presence of etruscus-like (elliptical) forms while in *U. spelaeus*, forms with a narrow or wide sinus on the labial border of the crown predominate.

In short, even taking into account the significant inter and intra-population morphological variability of teeth and cusps, the cave bear premolars and molars from the Ramp zone (LUR) of La Lucia cave can be ascribed to *U. deningeri* species. The cave bear remains from the Hall zone (LUS) can be identified as *Ursus spelaeus* representatives.

M_2 Cusp morphology		*U. d.* LUR	BB	*U. s.* LUS	*U. s.* KK	TT
Paraconid	1-2 blunt cusplets	26	44	9	100	58
	3-4 blunt cusplets	6	4	48		
	>4 blunt cusplets	1	5			
Protoconid	Single	18	12	1	42	11
	Single w. cusplet	8	19	17	14	47
	Single w. 2 cusplets	5	13		37	
	Complex	1				
Metaconid	Two cusps	2	1			
	Three cusps	13	18	13	121	50
	One cusp & cusplets	16	3	2	9	8
	Two cusps & cusplets	3	21	2	29	3
Entoconid	One cusp	6		6	3	
	Two cusps	18	19	10	101	13
	Three cusps	12	15	8	26	30
	Complex	2	5		16	12
Hypoconid	W. hypoconulid	6	25	8	129	36
	Hypoconulid absent	27	19	10	19	22

Table 13. Morphotypes of the cusps of the second lower molar. BB-Sima de los Huesos (Atapuerca), KK-Ekain Cave (Deba), TT- Reguerillo Cave (Madrid).

M_3 Crown outline	LUR	*U. d.* BB	LUS	*U. s.* KK	*U. s.* TT
Elliptical-broad talonid tip, labial sinus absent.	4	1		5	3
Elliptical-acute talonid tip, labial sinus absent.	4	8	2		
Narrow labial sinus and oblique lingual border			4	5	16
Narrow labial sinus and very oblique lingual border	2	1	2	4	8
Narrow labial sinus/straight lingual border	1	3	5	6	5
Broad labial sinus/acute talonid tip	3	11		14	4
Broad labial sinus/rounded talonid tip	12	30	5	30	15
Broad labial sinus/sinus at the talonid tip	1	8			12

Table 14. Morphotypes of the cusps of the third lower molar, BB-Sima de los Huesos (Atapuerca), KK-Ekain Cave (Deba), TT- Reguerillo Cave (Madrid).

Metrical analysis

As it can be observed in the inventory of findings, there is, with the exception of cheek teeth and metacarpal and metatarsal bones, a reduced number of skeletal elements; this makes it very difficult to carry out any metrical comparison based on them. Therefore, we only compared the metrical aspects of cheek teeth and paw bones. As reference values of *U. deningeri* we included those from La Sima de los Huesos (BB) and Santa Isabel cave (SI) which were described *in extenso* in TORRES (1989) and TORRES *et al.* (2001). For *Ursus spelaeus* we used a large sample comprising values for a several number of Spanish localities: Arrikrutz (AA), Reguerillo (TT), El Toll (XX), Eirós (EE), La Pasada (SS), Los Osos (TE) and Troskaeta (TR). For bivariate analyses we decided to group the *U. spelaeus* values of La Lucia Hall together with the ones of other localities because the inter-population differences are poorly marked. Likewise, *U. deningeri* values from La Sima de los Huesos (BB) and Santa Isabel cave (SI) were also grouped together. These bivariate analyses include the equiprobable ellipses (95%) which inside comprise 95% of the total sample, assuming they show a normal distribution. This method was proposed by CRAMER (1946) & DEFRISSE-GUSSENHOVEN (1955), and was successfully used for *U. deningeri* and *U. spelaeus* discrimination in TORRES & GUERRERO (1983). Multivariate analysis has not proven to be a good system for discriminating between the two species, and TORRES & GUERRERO (1993) demonstrated the peculiar paw anatomy of *Ursus spelaeus parvilatipedis* Torres morphology. In this paper the ellipse calculations were made using the STATISTICA statistical package.

Metapodial bones

For the description of the bivariate analyses (antero-posterior and transversal bone measurements against the bone total length) we chose the more representative graphs, avoiding the use of measurements which show high scattering. In a general sense, we can say that transversal measurements taken on proximal and distal epiphysis and diaphysis discriminate much better than anteroposterior ones. The clearest species discrimination is based on transversal measurements of the diaphysis and the distal epiphysis. This is due to the variable robustness of the muscular insertions, reflected in moderate to acute bony outgrowth (exostosis) during the ageing period. In some cases teratological characteristics appear, and have been described as osteoarthrosis (PÉREZ *et al.*, 1986). Venial cases of bony outgrowth cannot always be diagnosed by the naked eye, and this affects the measurement's accuracy. Nevertheless, in spite of some measurements discriminating much better than others, we selected an "assortment" of plots to show that the discrimination between species is clear using all the measurements (figure 4 A-E; figure 5 F-J).

First metacarpal: maximum transversal diameter of the proximal epiphysis vs. total length (A).

Second metacarpal: maximum transversal diameter of the diaphysis vs. total length (B).

Third metacarpal: maximum anteroposterior diameter of the diaphysis vs. total length (C).

Fourth metacarpal: maximum anteroposterior diameter of the proximal epiphysis vs. total length (D).

Fifth metacarpal: maximum transversal diameter of the distal epiphysis vs. total length (E).

First metatarsal: maximum transversal diameter of the distal epiphysis vs. total length (F).

Second metatarsal: maximum transversal diameter of the distal epiphysis vs. total length (G).

Third metatarsal: maximum transversal diameter of the distal epiphysis vs. total length (H).

Fourth metatarsal: maximum anteroposterior diameter of the distal epiphysis vs. total length (I).

Fifth metatarsal: maximum anteroposterior diameter of the diaphysis vs. total length (J).

The general trend of this group of graphs matches very well (now there are more available data) the graphs drawn in TORRES (1989):

Metacarpal and metatarsal bones of *Ursus deningeri* are clearly more slender than their homologues in *Ursus spelaeus*. The values from *U. s. parvilatipedis* from Troskaeta cave (TR) have not been distinguished, but they are shorter and broader (transversal diameters) than the typical *U. spelaeus* ones (cf. TORRES *et al.,* 1991).

The points representing measurements taken on metapodials of *U. spelaeus* from La Lucia (LUS) become confused with the cloud of points of the Iberian total sample and have not been identified with a singular sign.

The points representing metric relationships of *U. deningeri* metapodials from La Lucia Ramp (LUR) — open triangles — clearly group with *U. deningeri* ones from the total Iberian sample (La Sima de los Huesos (BB) and Santa Isabel (SI).

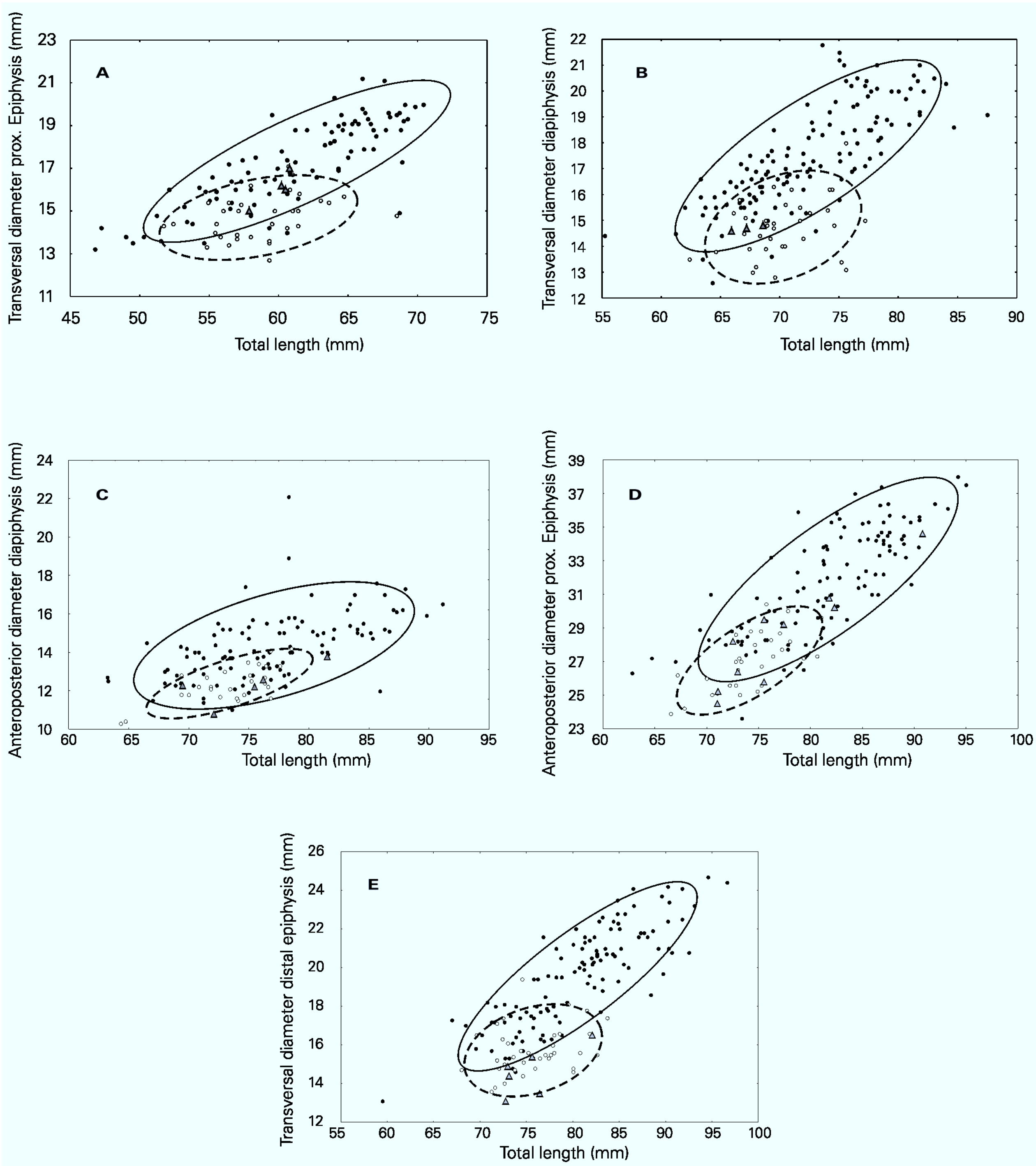

Figure 4.- Bivariate analysis of transversal and anteroposterior measurements against total length of different metacarpal bones. Equiprobable ellipses (95%) are included. (dashed line corresponds to *U.deningeri* samples, solid line corresponds to *U.spelaeus* samples). Dark circles represent the whole *Ursus spelaeus* Iberian sample. Light circles represent the whole *Ursus deningeri* Iberian sample. Triangles represent the La Lucia Ramp representatives measurements.
A-First metacarpal: maximum transversal diameter of the proximal epiphysis vs. total length;
B-Second metacarpal: maximum transversal diameter of the diaphysis vs. total length;
C-Third metacarpal: maximum anteroposterior diameter of the diaphysis vs. total length;
D-Fourth metacarpal: maximum anteroposterior diameter of the proximal epiphysis vs. total length;
E-Fifth metacarpal: maximum transversal diameter of the distal epiphysis vs. total length .
All measurements are in milimeters.

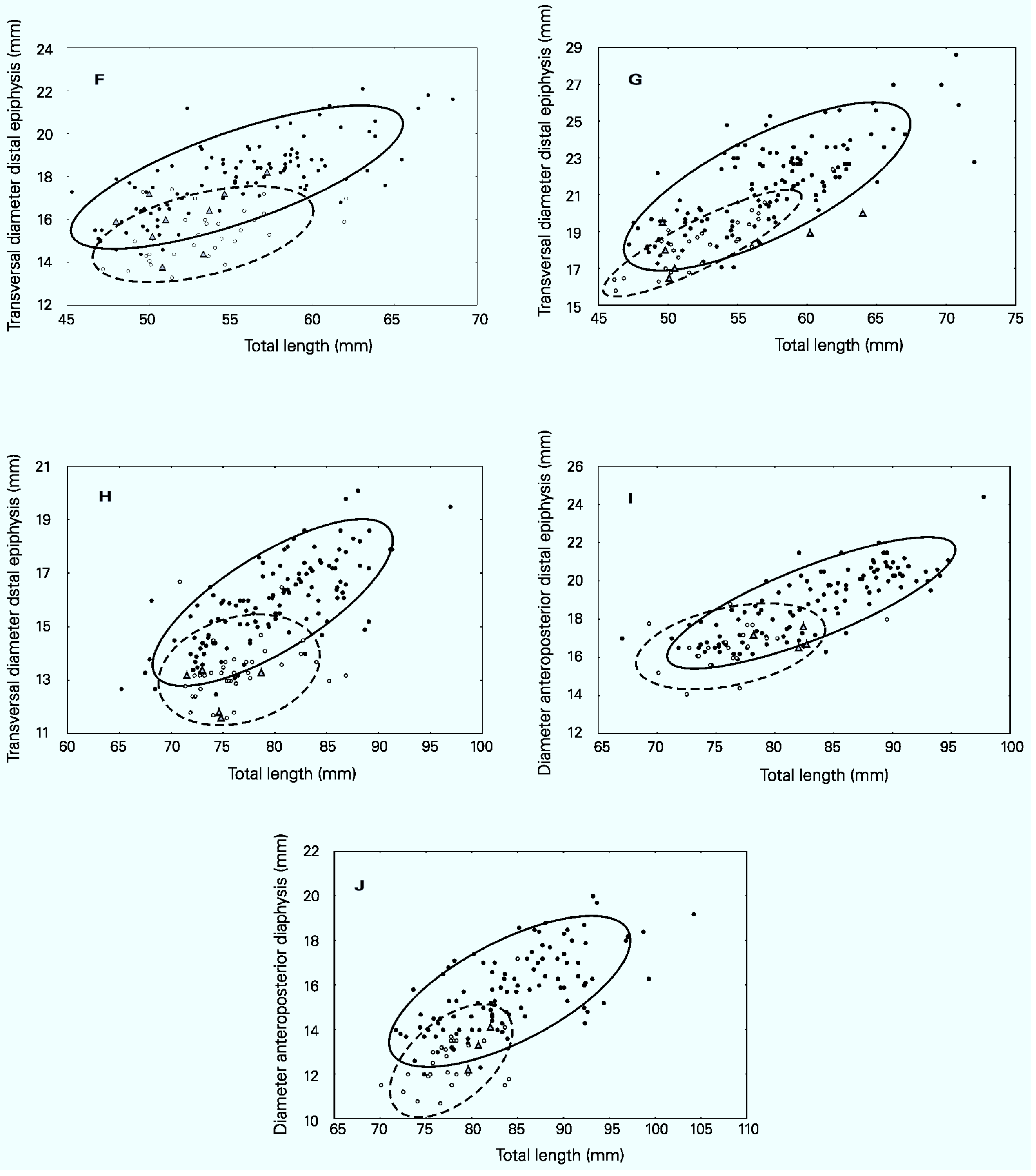

Figure 5.- Bivariate analysis of transversal and anteroposterior measurements against total length of different metatarsal bones.
Equiprobable ellipses (95%) are included (dashed line corresponds to *U.deningeri* samples, solid line corresponds to *U.spelaeus* samples). Dark circles represent the whole *Ursus spelaeus* Iberian sample. Light circles represent the whole *Ursus deningeri* Iberian sample.
Triangles represent the La Lucia Ramp representatives measurements.
F-First metatarsal: maximum transversal diameter of the distal epiphysis vs. total length;
G-Second metatarsal: maximum transversal diameter of the distal epiphysis vs. total length;
H-Third metatarsal: maximum transversal diameter of the distal epiphysis vs. total length;
I-Fourth metatarsal: maximum anteroposterior diameter of the distal epiphysis vs. total length;
J-Fifth metatarsal: maximum anteroposterior diameter of the diaphysis vs. total length.
All measurements are in milimeters.

According to the values of the regression coefficient (table 15) the correlation between the measurements taken on metapodial bones from *U. spelaeus* is reasonably high and extremely significant. The values of the regression coefficient in *U. deningeri* samples are lower than those in *U. spelaeus* and their significance is also lower. This may be due to their smaller sample size, although in some cases the lower values of the regression coefficient are highly significant. A twofold explanation can be offered here: *U. deningeri* was the first speloid species in the European Pleistocene realm. According to GARCÍA & ARSUAGA (2001) *U. deningeri savini* Andrews is, from a morphological point of view, quite different from the speloid species group and must be considered as separate (*Ursus savini*). It may be that the first "speloid experience" evolving towards wider paws reflected a morphological uncertainty, in which robust and slender forms coexisted in their populations. Another explanation lies in the characteristics of the *Ursus deningeri* sample, where there is an overwhelming influence of La Sima de Los Huesos (BB) measurements. This bear bone accumulation may represent a longer time span than previous *Ursus deningeri* remains, representing a diachronic accumulation mixed in a very jumbled way.

In all the selected cases the bivariate analysis of each pair of measurements consists of two clouds of points which correspond to each species. Both clouds of points are clearly distinguishable, although there is a minor overlap at their common fringe and, in almost all the cases, some *U. spelaeus* values appear scattered inside the cloud of points from *Ursus deningeri.*

The total length of the metapodial bones of *U. spelaeus* shows a noteworthy range length, such that the range of the total length of metapodials from *U. deningeri* turns out to be comfortably included in the distribution range of *U. spelaeus* values. Some *U. spelaeus* metapodials are even shorter than the shortest ones from *U. deningeri*. Nevertheless, *U. deningeri* metapodials are clearly more slender than *U. spelaeus* ones, as can be seen in the distributions of each cloud of points. Although one can doubt if the smaller *U. spelaeus* representatives correspond to immature bears, these metapodials showed completely fused epiphyses; however a tiny line reflected the ancient situation of the growth plate, as occurs in some of the bigger ones. We know of one case of retained ossification of the growth plates in almost all the skeleton elements (Amutxate cave, unpublished). However, because there is no gap in the size distribution, we interpret that these small sized bears were simply "very small cave bears".

The extremely wide range of the total length of *U. spelaeus* metapodials reflects an enormously well developed sexual dimorphism that is very well known in limb (KURTÉN, 1957; REISINGER & HOHENEGGER, 1998) and articular bones (QUILES & MONCHOT, 2004); the more robust ones correspond to hyper-males while the smaller ones correspond to hyper-females.

In *U. deningeri* sexual dimorphism does not seem to be so dramatically evident and their whole metapodial length range overlaps that of *U. spelaeus* females. Nevertheless, *U. deningeri* metapodials can be discriminated from their *U. spelaeus* homologs through their relative transversal and anteroposterior sizes. Multivariate analysis (TORRES & GUERRERO, 1993) also discriminated between cave bear species populations.

For the metrical analysis of dentition we chose an assortment of the many bivariate graphs that, *a priori* (TORRES, 1989), are known to differentiate the two speloid species.

The bivariate plot of length-maximum width of the upper carnassial (figure 6A) provides good differentiation between *Ursus deningeri* and *Ursus spelaeus;* there is only a small overlap between

	U. deningeri		*U. spelaeus*	
	N	r	N	r
McI (2/1)	102	0.8798 (p=0.000)	61	0.6440 (p=0.000)
McII (4/1)	134	0.6344 (p=0.000)	37	0.3229 (p=0.051)
McII (5/1)	107	0.5455 (p=0.000)	32	0.7011 (p=0.000)
McIV (3/1)	116	0.8117 (p=0.000)	40	0.8114 (p=0.000)
McV (5/1)	110	0.8232 (p=0.000)	41	0.3785 (p=0.015)
MtI (6/1)	108	0.7114 (p=0.000)	41	0.4171 (p=0.007)
MtII (6/1)	127	0.7458 (p=0.000)	33	0,7779 (p=0.000)
MtIII (4/1)	127	0.7246 (p=0.000)	42	0.2509 (p=0.109)
MtIV (7/1)	114	0.8108 (p=0.000)	24	0.3915 (p=0.000)
MtV (5/1)	110	0.6016 (p=0.000)	32	0.5449 (p=0.000)

Table 15. Correlation coefficients of the bivariate comparisons from metapodial bones

both clouds of points. The La Lucia values match totally with *Ursus deningeri* ones. The ranges of both measurements are quite similar in both species, the marked scattering visible in the length of *U. spelaeus* metapodials being unobservable. TORRES *et al.* (2002c) described how the lack of evident sex dimorphism in cheek teeth of *U. spelaeus. U. deningeri* points (La Lucia values included) clearly indicate that their upper carnassials are relatively broader than *U. spelaeus* ones, where a bigger absolute size is evident. This means that the typical cheek teeth enlargement in *U. spelaeus* was not accompanied by a similar augmentation in their labial-lingual width (negative allometry). On the other hand, the height of the cusps of the fourth upper premolars from *U. spelaeus* grew in a very marked way, being relatively higher than their counterparts in *U. deningeri.*

The bivariate analysis of the talus labial length against the total length of the first upper molar (figure 6B) reveals, in both species, that these measurements are highly correlated and that there is a small overlap. The values from La Lucia (LUR) match very well with the typical ones from La Sima de los Huesos (BB) and Santa Isabel (SI). The first upper molars from *U. spelaeus* appear to have an enlarged talus due to their growing crushing function (positive allometry). The talus width of the first upper molar of *U. deningeri* shows isometry when compared to that of *U. spelaeus* (figure 6C), while the width of the talus shows negative allometry, as occurs in the fourth upper premolar.

Figure 6D presents the bivariate analysis of the trigon width of the second upper molar against total length. The measurements taken on the second upper molars from La Lucia Ramp (LUR), as well as many measurements taken from representatives from La Sima de los Huesos and Santa Isabel, group with the narrower *U. spelaeus* second upper molars. This may be due to the large variability of the lingual cingulum in U. *U. deningeri,* which in some cases protrudes more than two millimeters from the general outline of the lingual side of the crown (see TORRES, 1989).

The total width of the fourth lower premolars of *Ursus spelaeus* shows a marked positive allometry (figure 6E), reflecting the size and number of cusplets that built the paraconid (many cusplets or large cusplets make an almost circular crown outline). The values measured in the La Lucia sample (LUR) match perfectly with the cloud of points representing the *U. deningeri* sample. The bivariate analysis of the paraconid height against the total length of the fourth lower premolar (figure 6F) clearly reflects the importance of this complex of cusplets in *U. spelaeus*, despite the lack of any functionality — this premolar is usually unworn. There are a number of premolars of *U. deningeri* in which the paraconid is totally absent. In *U. spelaeus* the paraconid is always present as a single or duplicated — even more complex – cusp. BARYSHNIKOV (1998) describes the fourth lower premolars of *U. deningeri* where the paraconid is absent.

There is a positive allometry in the distribution of the talonid length (labial) vs. total length in the first lower molar of *Ursus spelaeus* (figure 6G). This can be explained as a response to the necessary enlargement of the crushing area of the molar (CRUSAFONT & TRUYOLS, 1957). The overlap between *U. deningeri* and *U. spelaeus* clouds of points is not very important and the values taken on the La Lucia (LUR) representatives are comprised inside the *U. deningeri* cloud of points. There are no very marked differences between the distributions of the talonid width vs. total length, although there is a slight positive allometry in *U. spelaeus*, marking the relative widening of the talonid of the first lower molar to enlarge the occlusal area. This tendency can be visualized more clearly in the bivariate analysis of the distance between the entoconid and hypoconid apices against the talonid width (figure 6H). The graph reflects the real enlargement of the crushing area of the talonid through a verticalization of the cusps that, in *U. deningeri,* converged towards the labial-lingual axial plane in a more carnivorous-like architecture. The values from *U. deningeri* from the La Lucia Ramp (LUR) site appear clearly included in the *U. deningeri* cloud of points.

There are no special differences between the tendencies of both *U. deningeri* and *U. spelaeus* clouds of points representing the labial length of the trigonid vs. the total length of the second lower molar (figure 6I). In fact, this can be considered to be a case of isometry, though there is a clear metrical separation between both species and the La Lucia U. deningeri values match with the *U. deningeri* general distribution. The graph shows that in *U. deningeri* the relative trigonid width is greater than in *U. spelaeus*. In the graph of the bivariate analysis of talonid width against the total length of the molar (figure 6J) we can also observe a good fit of the La Lucia bear (LUR) values with the *U. deningeri* cloud of points, as well as a clear metrical separation between species and an almost isometrical relationship.

A very marked positive allometry in *U. spelaeus* is noticeable in the bivariate analysis of the third lower molar width against its total length (figure 6K). We consider this to be a geometrical

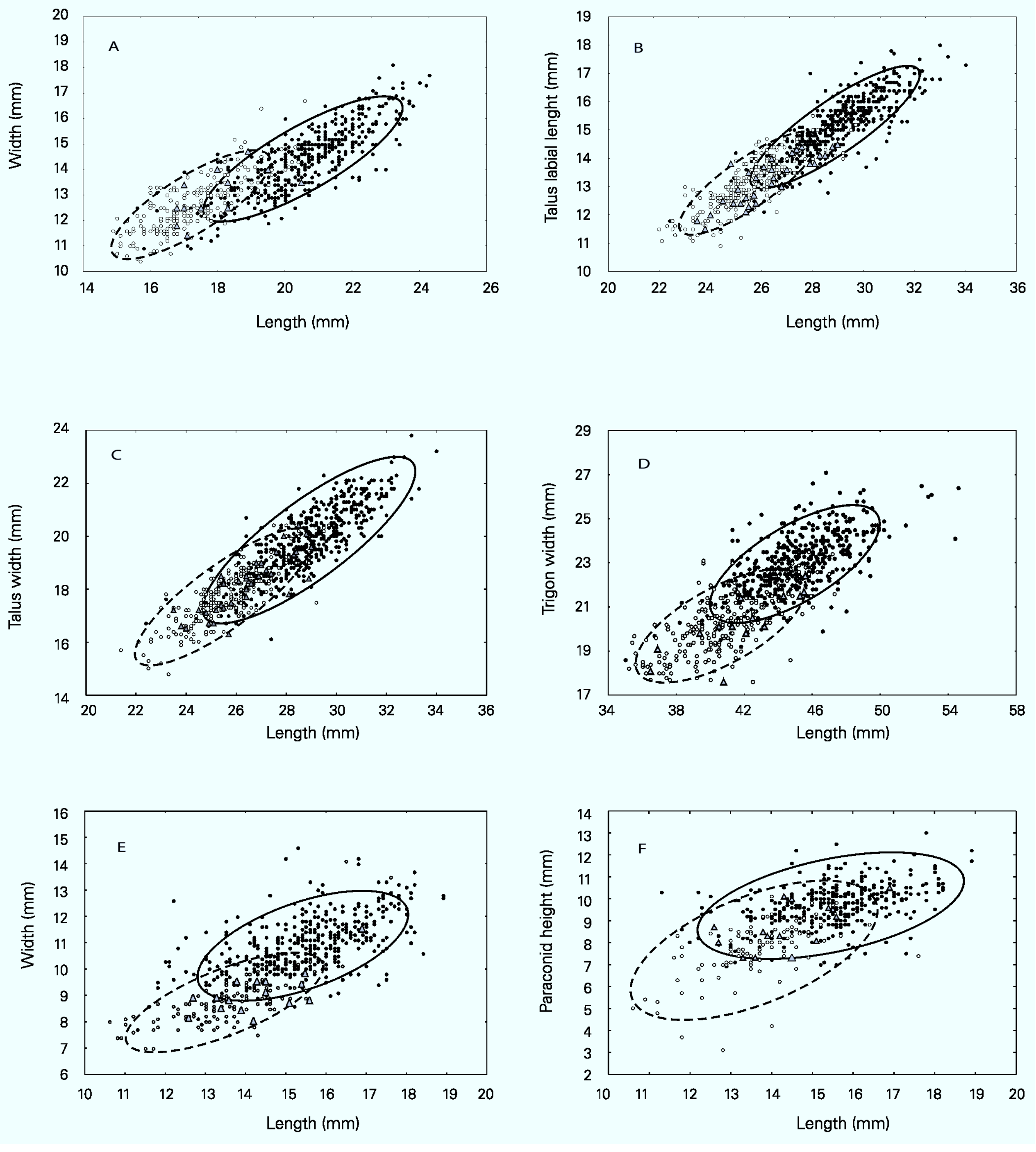

Figure 6.- Bivariate analysis of selected measurements taken on cheek teeth.
Equiprobable ellipses (95%) are included (dashed line corresponds to *U.deningeri* samples, solid line corresponds to *U.spelaeus* samples). Dark circles represent the whole Ursus spelaeus Iberian sample. Light circles represent the whole *Ursus deningeri* Iberian sample. Triangles represent the La Lucia Ramp representatives measurements.
A- Fourth upper premolar maximum width vs. total length;
B- First upper molar talus labial length vs. total length;
C- First upper molar talus width vs. total length;
D- Second upper molar trigon width vs. total length;
E-Fourth lower premolar: maximum width vs. total length;
F-Fourth lower premolar: paraconid height vs. total length.

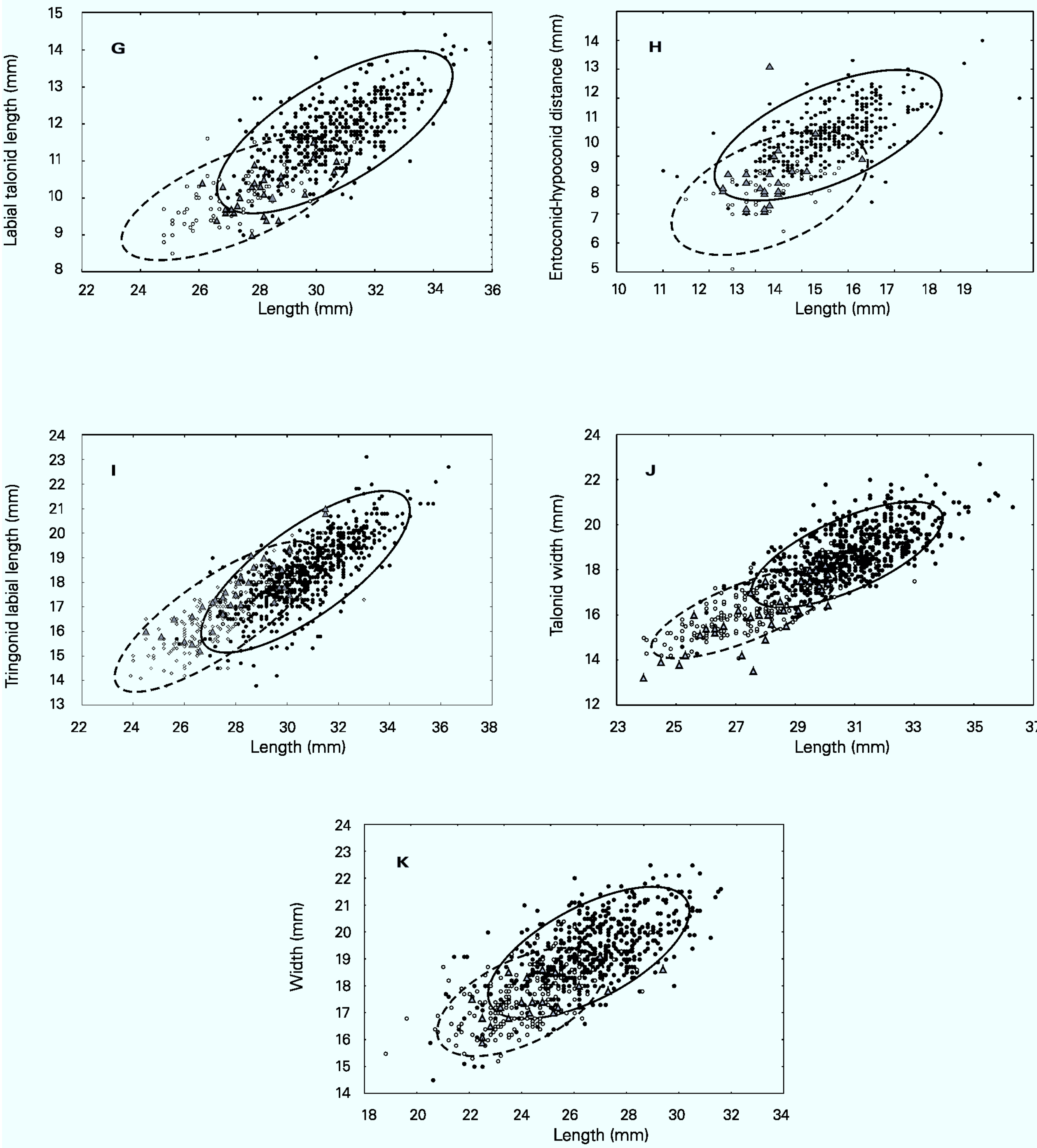

Figure 6 (cont)
G-First lower molar labial talonid length vs. total length;
H-First lower molar entoconid-hypoconid distance vs. talonid width;
I-Second lower molar: trigonid labial length vs. total length;
J-Second lower molar: talonid width vs. total length;
K-Third lower molar maximum width vs. total length.

response to the enlargement of the talus of the second upper molar. At a specific level there is good differentiation between both species but they are bears (*U. spelaeus*) with very small third lower molars. In fact, EHERENBERG (1931) (in ERDBRINK, 1953) described some extremely small teeth from the site of Drachenhöle (Mix nitz, Austria) as "something different", and rejected including them in the species variability range. We have found these teeth, sometimes extremely small, sometimes extremely big, elsewhere and consider them to be the tails of an ideal normal size distribution. The sizes of the third lower molars from the La Lucia Ramp (LUR) confirm their attribution to *U. deningeri* species.

CONCLUSIONS

There are some visible, but not very important, differences between ESR ages and those from AARD. This is because the ESR ages were used to determine the best fitted age calculation algorithms (highest correlation coefficient value) for AARD and the final age cannot exactly match with the radiometric one. Nevertheless, the La Lucia Ramp accumulation took place during the 9th OIS, while the La Lucia Hall (LUS) accumulation corresponds to the 5th OIS. It seems obvious that there are two highly chronologically distinctive cave bear populations at the La Lucia cave, and that the time gap between them can be estimated to be a minimum of 200 ka. We cannot discard the possibility that across this time span other cave bear accumulations took place, but these may be inaccessible or have been destroyed after local hydrological reactivations, as is currently happening in the Ramp site.

The La Lucia Ramp (LUR) site bears can undoubtedly be identified as *Ursus deningeri* Von Reichenau because they group very well in morphological and metrical aspects. The cave bear remains from La Lucia Hall (LUS) belong to the *Ursus spelaeus* Rosenmüller-Heinroth species group.

It seems that the La Lucia Ramp (LUR) accumulation corresponds to a prolonged time span when different cave occupations by adult bears, both males and females, succeeded each other. This scenario seems not to be applicable to the La Lucia Hall (LUS) accumulation, where findings suggest a short colonization by pregnant females accompanied by cubs and yearlings.

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